African Invertebrates Vol. 48 (1) Pages 87–101 Pietermaritzburg April, 2007

A review of the South American Palaeozoic entomofauna Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa

R. G. Martins-Neto[1], O. F. Gallego[2], C. Brauckmann[3] and **J. L. Cruz[4]**

[1]Programa de Pós-graduação em Ciências Biológicas, Comportamento e Biologia Animal, Universidade Federal de Juiz de Fora; Sociedade Brasileira de Paleoartropodologia, Campus Universitário-Martelos, 36036-900, Juiz de Fora, MG, Brasil – Centro de Ensino Superior de Juiz de Fora / CESJF; martinsneto@terra.com.br
[2]Paleontología (Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste) y Área Paleontología (Centro de Ecología Aplicada del Litoral, CONICET), Casilla de Correo 128, 3400 Corrientes, Argentina; ofgallego@hotmail.com
[3]Institut für Geologie und Paläontologie, TU Clausthal, Leibnizstrasse 10, D-38678 Clausthal-Zellerfeld, Germany; carsten.brauckmann@tu-clausthal.de
[4]Granaderos 1519; 5500, Mendoza, Argentina; cruzruiz@ciudad.com.ar

ABSTRACT

Four new genera of the family Proedischiidae Pinto & Ornellas, 1978 are described from the Upper Carboniferous of the Bajo de Véliz locality (Argentina): *Velizphlebia cruzi* gen. et sp. n., *Paganzophlebia polyclada* gen. et sp. n., *Irajanarkemina* gen. n. (type species *Narkemina rodendorfi* Pinto & Ornellas, 1978), *Argentinonarkemina* gen. n. (type species *Paranarkemina amosi* Pinto, 1992). The position of the genus *Proedischia* Pinto & Ornellas, 1978 from the Upper Carboniferous, Paraná Basin, is discussed, and Narkeminidae Pinto & Ornellas, 1991 is synonymised with Proedischiidae. Taiophlebiidae fam. n. is described from the Upper Carboniferous of Brazil. New combinations are proposed: *Carpenteroptera rochacamposi* (Pinto & Ornellas, 1978), comb. n., is transferred from the genus *Narkemina* Martynov, 1930 to the genus *Carpenteroptera* Pinto, 1990 (family Carpenteropteridae); *Taiophlebia ferreirai* (Pinto, 1994), comb. n., from the genus *Archaemegaptilus* Pinto, 1994 to the genus *Taiophlebia* gen. n. (family Taiophlebiidae); and *Carpenteroptera rochacamposi* (Pinto & Ornellas, 1978), comb. n., from the genus *Narkemina* to the genus *Carpenteroptera* Pinto, 1990 (family Carpenteropteridae).

KEY WORDS: Insects, Carpenteropteridae, Proedischiidae, Taiophlebiidae, Carboniferous, South America, Argentina, Bajo de Véliz, Brazil, Paganzo Basin, new taxa, new synonymy, new combinations.

INTRODUCTION

As shown in the compilation by Pinto and Adami-Rodrigues (1999) and additions by Pinto *et al.* (2000), Pinto and Sedor (2000), Pinto and Adami-Rodrigues (pers. comm., 2005), the South American Palaeozoic entomofauna is largely diverse, including a rather great number of previously described taxa. But only a few of them are documented by more than a single specimen. This means that more specific field investigations and prospecting work might supply us with a still more diverse insect fauna. In particular, specific Konservat-Lagerstätten for Palaeozoic insects, like those known for younger strata (e.g. the Early Cretaceous Santana area in north-eastern Brazil), are still needed in South America.

The relevant localities are concentrated in southern South America (Paraná Basin of southern Brazil and Uruguay; Paganzo Basin and Central Patagonian Basin in Argentina; Islas Malvinas). One of the localities within the Paganzo Basin—Cuestita de la Herradura near Malazán, La Rioja Province—belongs to the stratigraphically oldest hitherto-known insect-bearing localities (Brauckmann *et al.* 1996).

The present contribution is the first part of a planned series dealing with a detailed systematic review of South American Palaeozoic insects, and is focused on the Ischnoneuroidea–Cacurgoidea complex.

This complex is often controversially discussed in the literature. Martynov (1930) distinguished seven groups within the former "Paraplecoptera", among them the Cacurgoidea which included the families Cacurgidae, Narkemidae and Omaliidae. Sharov (*apud* Storozhenko 1997*b*) proposed the subdivision of the order Paraplecoptera into six superfamilies, among them the Cacurgoidea, including the same three families as in Martynov. Rasnitsyn (*apud* Storozhenko 1997*b*), however, included the Narkemidae within the Grylloblattida Walker, 1914, whereas Storozhenko (1997*b*) considered the Narkemidae as insects *incertae sedis* and also included the Narkeminidae in Grylloblattida.

Rasnitsyn (2002) considered the Narkeminidae, together with the Aetophlebiidae Handlirsch, 1906, as junior synonyms of the Ischnoneuridae Handlirsch, 1906, and attributed them together with the Spanioderidae, Cacurgidae and *Eoblatta* to the eoblattid–spanioderid–cacurgid–narkeminid assemblage of the order Eoblattida.

The adopted terminology of the venation follows Kukalová-Peck (1991).

GEOGRAPHICAL POSITION AND GEOLOGICAL SETTING

Velizphlebia cruzi gen. et sp. n. and *Paganzophlebia polyclada* gen. et sp. n. come from the Bajo de Véliz Formation (Paganzo Basin), San Luis Province (Argentina). This formation crops out at the Bajo de Véliz locality (Fig. 1), which is situated at the north-eastern section of the Sierra Grande de San Luis (32º15'S:65º31'W), about 25 km west of the village of Santa Rosa. Geologically, the Bajo de Véliz Formation (Flores 1969) unconformably overlies the metamorphic basement (composed by greenish phyllites and micaschistes); its thickness is about 164 m. From the bottom to the top three members can be distinguished: (a) Cautana Member (102 m), composed of a basal polymictic conglomerate, thick beds of greenish siltstones with concretions, fine compact greenish-grey sandstone with ondulites and finally a potent series of thick beds of massive arkosic sandstones (light grey and yellow) with thin intercalations of green and delicately stratified siltstones; (b) Pallero Member (53 m), mainly composed of a greyish to greenish shaly siltstone, laminated and with interbedded sandstones, and light greenish, greyish to dark laminated siltstones with beds of dark grey clayey shaly slates, interbedded by fine grained hard sandstones, sometimes calcareous (10–20 cm); (c) Lomas Member (9 m), represented by yellowish to light greenish-brown sandstone of medium to coarse grains in compact beds (0.5–1 m) with crossbedding stratification (Fig. 1B; Hünicken & Pensa 1975; Pinto & Ornellas 1978).

The Pallero Member is uniquely rich in fossils. The fossils include plant macrofossils, palynomorphs, seeds, stems, insects and arachnids. Since the 19th century (Kurtz 1895), different authors have described the geological and palaeontological aspects of this formation in many papers. Compilations were published by Hünicken and Pensa (1975), Hünicken *et al.* (1981), Archangelsky *et al.* (1995,1996), and Azcuy *et al.* (1987).

The Bajo de Véliz Formation has been dated ranging from late Upper Carboniferous to early Lower Permian, up to Upper Permian. The Late Carboniferous age was based on the insect and arachnid assemblage proposed by Pinto and Ornellas (1978, 1980) and Pinto and Hünicken (1980). Azcuy and Jelín (1980) also suggested its probable

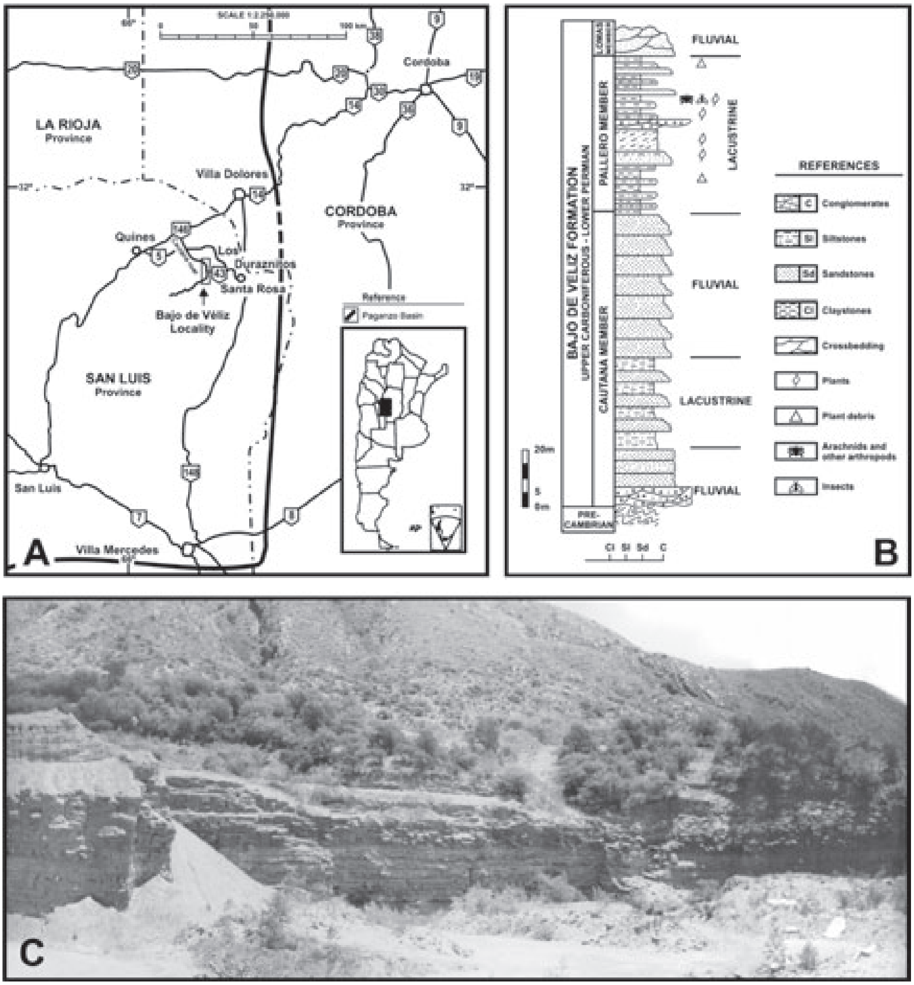

SCALE 1:2.250.000
0
50
100 km
LA RIOJA
Province
CORDOBA
Province
SAN LUIS
Province
Cordoba
Villa Dolores
Quines
Los Duraznitos
Santa Rosa
Bajo de Véliz
Locality
San Luis
Villa Mercedes
Reference
Paganzo Basin
32°
66°
A
FLUVIAL
LACUSTRINE
FLUVIAL
LACUSTRINE
FLUVIAL
BAJO DE VELIZ FORMATION
UPPER CARBONIFEROUS - LOWER PERMIAN
PALLERO MEMBER
CAUTANA MEMBER
PRE-CAMBRIAN
20m
5
0m
Cl Sl Sd C
REFERENCES
Conglomerates
Siltstones
Sandstones
Claystones
Crossbedding
Plants
Plant debris
Arachnids and other arthropods
Insects
B
C

Fig. 1. Bajo de Véliz locality, San Luis province, Argentina: (A) Location map; (B) Stratigraphic section (both adapted from Hünicken & Pensa 1975; Pinto & Ornellas 1978; Azcuy *et al*. 1987); (C) Partial view of a quarry of the outcrop.

Late Carboniferous age (late Stephanian) based on the palynoflora. The fossil plants include species of the *Gangamopteris* biozone and their content corresponds to the Lubeckense flora (Archangelsky & Cúneo 1984; Archangelsky *et al.* 1995, 1996) that corresponds to the Carboniferous–Permian boundary. The palynoflora suggested different age such as Permian (Sakmarian; Menéndez 1971) or earliest Permian (Gutiérrez & Césari 2000). Radiometric dating of other correlated units (e.g. La Colina, La Rioja Province) brings a middle Stephanian age (295 ± 6 Ma, Late Carboniferous; Archangelsky *et al.* 1995). The age of the basement of the Sierra Grande de San Luis is established between 330 and 300 Ma, i.e. Early to Late Carboniferous. Finally the consensus considered the age of the Bajo de Véliz Formation ranging from the latest Carboniferous to the earliest Permian (Gutiérrez 2006).

TAXONOMY

Cohort Polyneoptera *sensu* Gorochov 2001
(= Gryllones *sensu* Rasnitsyn 2002; = Panorthoptera *sensu* Béthoux & Nel 2002)
Order Grylloblattida Walker, 1914 (= Eoblattida *sensu* Rasnitsyn 2002, *partim*)

Superfamily Ischnoneuroidea Handlirsch, 1906, **stat. n.**

Diagnosis: Fore wing with ScP distally fused with RA. CuA short, distally fused with the basal part of MP+CuA.

Constituent families: Ischnoneuridae Handlirsch, 1906; Proedischiidae Pinto & Ornellas, 1978; Taiophlebiidae fam. n.; Spanioderidae Handlirsch, 1906.

Family Proedischiidae Pinto & Ornellas, 1978

Proedischiidae: Pinto & Ornellas 1978: 309 (type genus *Proedischia* Pinto & Ornellas, 1978).
Narkemocacurgidae: Pinto & Ornellas 1978: 310 (not based on valid genus name); 1981: 108.
Narkeminidae: Pinto & Ornellas 1991: 93 (type genus *Narkemina* Martynov, 1930); Storozhenko 1996: 18; 1997*b*: 4; 1998: 69. **Syn. n.**
Narkemidae: Handlirsch 1911: 322 (part.); Martynov 1930: 1229 (part.); Storozhenko 1997*a*: 63 (part.).
Ischnoneuridae: Rasnitsyn 2002: 258 (part.).

Diagnosis: Fore wing with the presence of r–m in the distal part of MA. MP+CuA sigmoid, convergent to MA.

Constituent genera: *Narkemina* Martynov, 1930 (Upper Carboniferous, Kuznetzk Basin, Russia), *Narkeminopsis* Whalley, 1979 (Upper Carboniferous of Great Britain), *Irajanarkemina* gen. n. (Upper Carboniferous, Paraná Basin, Brazil), *Paranarkemina* Pinto & Ornellas, 1980 (Upper Carboniferous, Argentina and Brazil), *Velizphlebia* gen. n. (Upper Carboniferous, Argentina), *Argentinonarkemina* gen. n. (Upper Carbo-niferous, Argentina), *Proedischia* Pinto & Ornellas, 1978 (Upper Carboniferous, Brazil), and *Paganzophlebia* gen. n. (Upper Carboniferous, Argentina). According to Rasnitsyn (pers. comm.), judging from Béthoux and Nel (2005), *Bouleites* Lameere, 1917 could also belong to Narkeminidae (however not examined).

Remarks: Pinto and Ornellas (1978) proposed the family name Narkemocacurgidae for *Narkemina* Martynov, 1930 and related genera to highlight the transitional characters. But since this was not in accordance with the *International Code of Zoological Nomenclature* (ICZN 1985), the same authors (Pinto & Ornellas 1991) replaced this name with Narkeminidae. This was overlooked by Storozhenko (1996), when he also changed the family name into Narkeminidae. As noted below, however, the correct family name for the taxon as defined in this paper is Proedischiidae Pinto & Ornellas, 1978.

The Proedischiidae share a very striking common character in the fore wing: MP+CuA convergent to MA (in some included taxa within the family, this vein is strongly convergent). This feature is not present within the *Ischnoneura–Spaniodera–Cacurgus–Eoblatta* complex, and therefore we do not regard the Proedischiidae and Ischnoneuridae as synonymous as Rasnitsyn (2002) did. Rasnitsyn (pers. comm.), after examining the type genus, considers Aetophlebiidae Handlirsch, 1906 as fitting the diagnosis of Proedischiidae perfectly (cf. original description of *Aetophlebia singularis* by Scudder, 1885, fig. 9). If so, it could be concluded that Proedischiidae is a junior synonym of Aetophlebiidae, the older name. However, the type genus as figured by Handlirsch

(1906–08, pl. XVI, fig. 14) neither has ScP distally fused nor the typical short CuA distally fused with MP+CuA, as proposed here for the Proedischiidae, so excluding it from the Proedischiidae.

Genus **Irajanarkemina** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: In honour of Prof. Dr Irajá Damiani Pinto (UFRGS, Brazil), the first and outstanding scientific investigator of the South American Palaeozoic entomofauna, and *Narkemina*, the closely related genus. Gender feminine.

Type species: *Narkemina rodendorfi* Pinto & Ornellas, 1978, designated here.

Diagnosis: Fore wing relatively wide. ScP distally fused with RA. Origin of RP close to apex of wing, far from origin of MP. MP+CuA strongly convergent to MA with the secondary branches notably curved toward the anal margin. Supporting cross veins r–m and ma–mp present. Origin of CuP not directly from the distal part of CuA.

Discussion: *Irajanarkemina* gen. n. differs from *Narkemina*, the closest genus, by having a wider fore wing (relatively narrow in the hitherto known species of *Narkemina*), MP+CuA less strongly convergent to MA, the secondary branches of which are notably curved toward the anal margin (Fig. 2) (straight and oblique to the anal margin in *Narkemina*).

Species included: Type species only.

Irajanarkemina rodendorfi (Pinto & Ornellas, 1978), **comb. n.**

Fig. 2

Narkemina rodendorfi: Pinto & Ornellas 1978: 311, pl. I, figs 4, 5; pl. II, figs 2, 3 (holotype MP-I-5283a, b; São Paulo, Upper Carboniferous; in UFRGS, Brazil; studied); Storozhenko 1998: 71, fig. 114.

Narkemina rohdendorfi: Pinto 1995: 47 (unjustified emendation); Pinto & Adami-Rodrigues 1999: 122 (unjustified emendation).

Remarks: In the original description, Pinto and Ornellas (1978) considered the holotype specimen as a hind wing. The absence of a typical anal fan as known from typical hind wings of other species of the Proedischiidae leads us to regard it more likely as a fore wing, however.

Pinto and Ornellas (1978) originally spelled the specific name "*rodendorfi*" which is possible if it is derived directly from the Russian (Cyrillic) spelling. Later the authors changed it to "*rohdendorfi*", the spelling which B.B. Rohdendorf himself preferred to use in transliterations of his name. According to Article 32.5.1 of the *International*

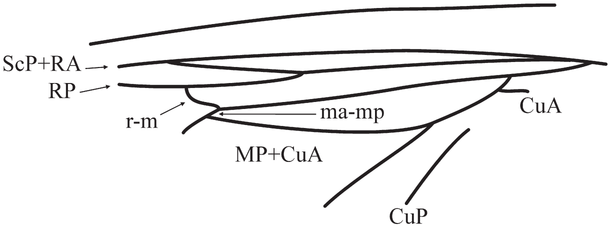
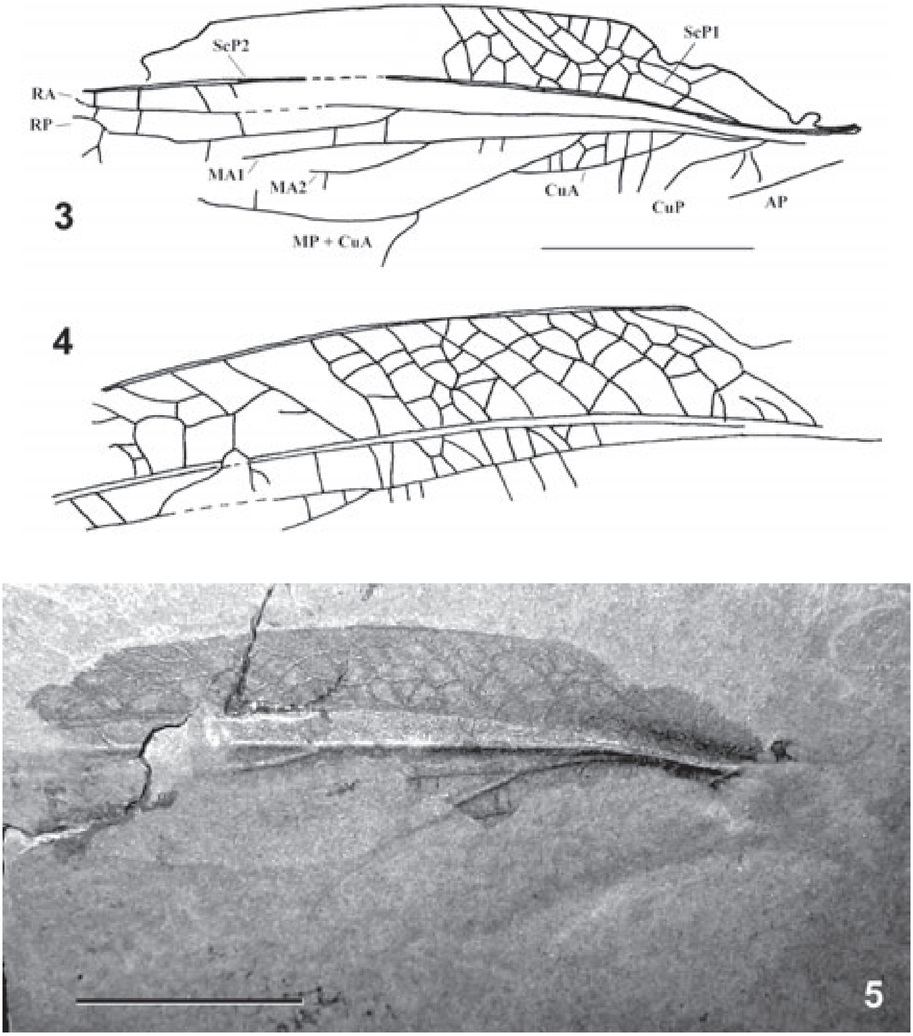


Fig. 2. *Irajanarkemina rodendorfi*, main venational pattern, schematic drawing. CuA, CuP, anterior and posterior cubitus; MA, MP, anterior and posterior media; RA, RP, anterior and posterior radius; ScA, ScP, anterior and posterior subcosta; r–m, supporting cross vein radius–media; ma–mp, supporting cross vein anterior–posterior media.



Figs 3–5. *Velizphlebia cruzi* gen. et sp. n., holotype, MHIN-UNSL-GEO-I 484: (3) wing venation; (4) details of costal area; (5) general appearance of specimen. Vein designations: see Fig. 2. Scale bars = 10 mm.

Code of Zoological Nomenclature (ICZN 1999), incorrect transliteration is not an inadvertent error and therefore does not require correction.

Genus **Velizphlebia** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: After the Bajo de Véliz locality, Argentina, and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *Velizphlebia cruz*i sp. n., designated here.

Diagnosis: Forewing relatively wide. Very wide and reticulate costal space and very basal MA fork. ScP distally fused with RA. Origin of RP at mid-length of the wing and far from origin of MP. MP+CuA strongly convergent to MA. Origin of CuP not directly from distal part of CuA.

Discussion. Similar to *Narkemina* and *Irajanarkemina* in having ScP distally fused with RA and MP+CuA strongly convergent to MA; differing however in having the origin of RP relatively far from the wing apex (although also far from the origin of MP) and the origin of CuP not directly from the distal part of CuA. Additionally the very wide and reticulate costal space and very basal MA fork are features completely different from the rest of the Proedischiidae.

Velizphlebia cruzi Martins-Neto, Gallego & Brauckmann, sp. n.

Figs 3–5

Etymology: In honour of Lic. Jorge Cruz (Mendoza, Argentina) who collected the specimen.

Description: Preserved length, 50 mm. Costal area relatively wide and filled with anastomosed cross-veins (Fig. 4). ScP1 conspicuous at the wing base and ScP distally fused with RA which is slightly curved. Origin of RP near mid-length of wing, apparently unbranched. MA two-branched. MP+CuA strongly convergent to MA. CuA short, distally fused with MP. CuP not directly branching from distal part of CuA.

Holotype: MHIN-UNSL-GEO-I 484, Museo de Historia Natural de la Universidad Nacional de San Luis, Geología; fragment of fore wing. ARGENTINA: Bajo de Véliz locality; Upper Carboniferous to Lower Permian, Pallero Member, Bajo de Véliz Formation.

Genus *Paranarkemina* Pinto & Ornellas, 1980

Paranarkemina: Pinto & Ornellas 1980: 288.

Type species: *Paranarkemina kurtzi* Pinto & Ornellas, 1980, by original designation.

Emended diagnosis: Fore wing relatively wide. ScP distally fused with RA. Origin of RP close to the origin of MP. MP+CuA not strongly convergent to MA. Supporting cross vein ma–mp absent. CuP convergent and distally fused with AP.

Comparison: *Paranarkemina* differs from the other known genera of the Proedischiidae, except *Argentinonarkemina* gen. n., in having the origin of RP close to the origin of MP. See schematic pattern of the main veins in Fig. 6.

Constituent species: *P. kurtzi* Pinto & Ornellas, 1980 (= *P. velizensis* Pinto & Ornellas, 1981) (Upper Carboniferous, Argentina) and *P. martinsnetoi* Würdig, Pinto & Adami-Rodrigues, 1998 (Upper Carboniferous, Paraná Basin, Brazil).

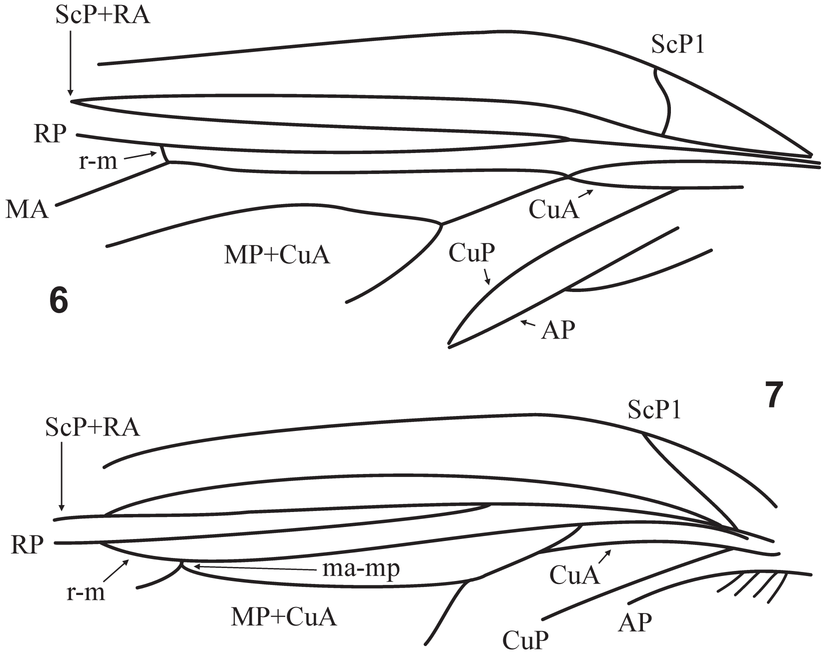
Remarks: Storozhenko (1998) considered *Paranarkemina velizensis* as a fragment of the hind wing of the last-instar subimago of *P. kurtzi* and synonymised both species, with which we agree.

Genus **Argentinonarkemina** Martins-Neto, Gallego & Brauckmann, gen. n.

Fig. 7

Etymology: After Argentina, where the material comes from, in combination with *Narkemina*. Gender feminine.

Type species: *Paranarkemina amosi* Pinto, 1992, here designated.



Figs 6, 7. Schematic drawing of wing venation: (6) *Paranarkemina martinsnetoi*; (7) *Argentinonarkemina amosi*. Vein designations: see Fig. 2.

Diagnosis: Origin of RP close to origin of MP. MP+CuA strongly convergent to MA, ma–mp present and CuP not distally fused with AP.

Comparison: Similar to *Paranarkemina* in having the origin of RP close to the origin of MP, differing however by having MP+CuA strongly convergent to MA, and ma–mp present, as well as CuP not distally fused with AP.

Species included: *Argentinonarkemina amosi* (Pinto, 1992), **comb. n.**

Genus *Proedischia* Pinto & Ornellas, 1978

Proedischia: Pinto & Ornellas 1978: 309.

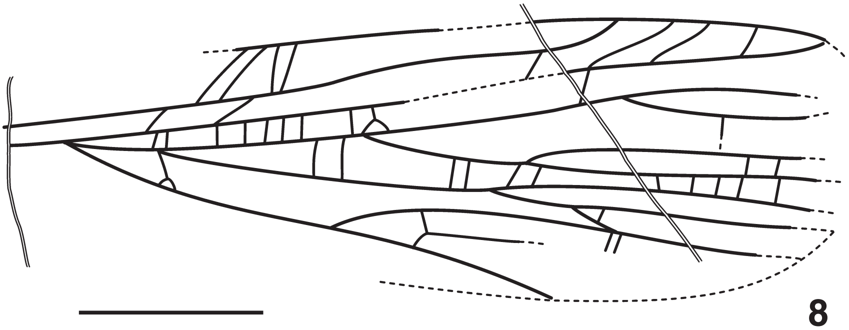
Type species: *Proedischia mezzalirai* Pinto & Ornellas, 1978, by original designation.

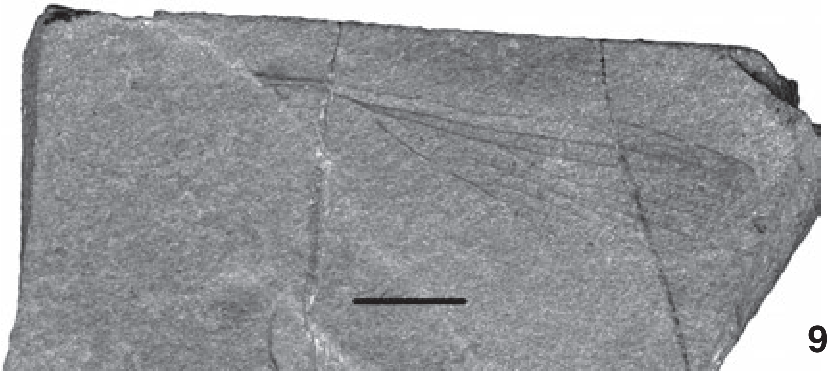
Emended diagnosis: Hind wing long and relatively narrow. ScP not distally fused with RA, but RA distally fused with RP. Origin of RP at mid-length of wing. Supporting cross vein r–m present, forming a conspicuous jugum-like constriction between RP and MA.

Comparison: *Proedischia* differs from *Narkemina* by having ScP not distally fused with RA and the origin of RP far from the wing base (very close to the wing base in *Narkemina* species).

Species included: Type species only.

Remarks: Pinto and Ornellas (1978) originally described this wing as a forewing belonging to the "Protorthoptera", and established a separate family Proedischiidae. But there are striking similarities with the Narkeminidae, as for example the long and





Figs 8, 9. *Paganzophlebia polyclada* gen. et sp. n., holotype, MHIN-UNSL-GEO-I 485: (8) details of venation; (9) general appearance of specimen. Scale bar = 10 mm.

oblique CuA. The main differences between *Proedischia* and *Narkemina* are restricted to the lack of a distal fusion of ScP and RA in *Proedischia*. This character removes it from *Narkemina* (with the best-known hind wings). Judging only from the position and course of RP, *Proedischia mezzalirai* could be attributed to the genus *Velizphlebia*. But in the hitherto-known species the position and course of these veins are different in the fore and hind wings. Therefore we prefer to maintain *Proedischia* as a separate genus until more complete material is available, but regard the family Proedischiidae as synonymous with the Narkeminidae. If so, the name Proedischiidae established in 1978 has priority.

Genus **Paganzophlebia** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: After the Paganzo Basin, Argentina, where the material comes from, and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *Paganzophlebia polyclada* sp. n., here designated.

Diagnosis: ScP distally sigmoid, not fused distally with RA. RP originating at wing mid-length. RA and RP distally branched, not fusing.

Comparison: Similar to *Proedischia* in having the hind wing with ScP not fused distally with RA and the origin of RP at the mid-length of the wing, but markedly differing in the distally sigmoidal ScP and distally branched and not fusing RA and RP.

Species included: Type species only.

Remarks: The specimen presents another hind wing of strong narkeminid affinities which cannot be exactly placed into a described genus. In several aspects the new taxon closely resembles the hind wings of the species of *Narkemina*, except for the absence of the distal fusion of ScP and RA. In this character, *Paganzophlebia* is similar to *Proedischia*, but it clearly differs from the latter in the much more slender shape which is more similar to typical members of the Proedischiidae. This is why we prefer to establish a separate genus. Future additional material should show if it could be maintained.

Paganzophlebia polyclada Martins-Neto, Gallego & Brauckmann, sp. n.

Figs 8, 9

Etymology: From Greek *poly* (many) and *clados* (branch), after the rich venation of the holotype specimen; here used as an adjective.

Description: Preserved length, 53 mm. ScP slightly sigmoidal, not distally fused with RA. RP two-branched, each branch distally dichotomising. Origin of RP very close to the wing base. MA simple, MP two-branched, with MP2 short, distally fused with CuA1. CuA long, slightly curved: CuA1 long and parallel to MP2; CuA2 shorter than CuA1, oblique to the anal margin.

Holotype: MHIN-UNSL-GEO-I 485, Museo de Historia Natural de la Universidad Nacional de San Luis, Geología; hindwing fragment, CuP not preserved. ARGENTINA: Bajo de Véliz locality; Upper Carboniferous to Lower Permian, Pallero Member, Bajo de Véliz Formation.

Family **Taiophlebiidae** Martins-Neto, fam. n.

Type genus: *Taiophlebia* Martins-Neto, gen. n.

Diagnosis: Fore wing with ScP and RA distally fused and RP multi-branched. RP origin at 1/5 of the wing base.

Genus **Taiophlebia** Martins-Neto, gen. n.

Taiophlebia: Martins-Neto *et al.*, 2004: 45.

Etymology: From the type locality and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *T. niloriclasodae* Martins-Neto, sp. n., by present designation.

Diagnosis: Fore wing with more than 100 mm long. Costal margin straight. Sc branching in ScA and ScP. ScP with at least two strong secondary branches. ScP/RA fused circa 1/4 of the wing apex. CuA most proximal branch reaches the anal margin after the wing midlength.

Species included: The type species and *Taiophlebia ferreirai* (Pinto, 1994), comb. n.

Remarks: *T. niloriclasodae* from the upper part of the Rio do Sul Formation at the Taió municipality, Santa Catarina, Brazil (Upper Carboniferous, Paraná Basin) is a key taxon for the understanding of the Ischnoneuroidea–Cacurgoidea complex. Particular characters of the venation such as the distal fusion of ScP and RA, and RP originating close to the basal fifth of the wing support a closer relationship to the representatives of the Ischnoneuroidea (Grylloblattida *sensu* Storozhenko), rather than to the Cacurgoidea

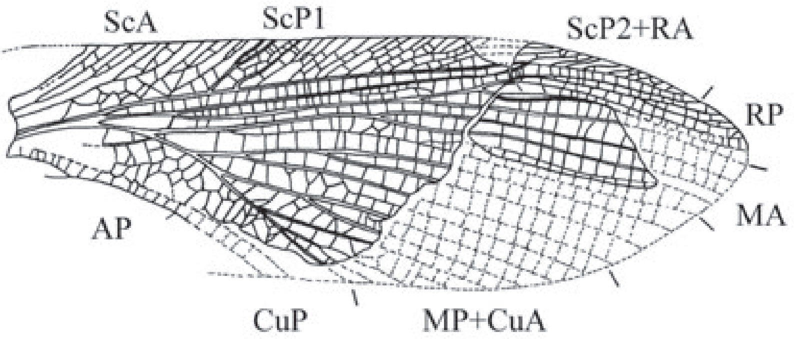


Fig. 10. *Taiophlebia niloriclasodae*, reconstructed forewing (after Dutra *et al*. in press). Vein designations: see Fig. 2.

("Paraplecoptera" *s.l.* or Orthoptera). The Taiophlebiidae differ from the Proedischiidae as well as from their closest related families by the lack of the typical convergence of MP+CuA and thus represent the most basal group within the Ischnoneuroidea–Cacurgoidea complex. Another genus, *Cacurgulopsis* Pinto & Adami-Rodrigues, 1995 from Boituva, São Paulo (Paraná Basin, Upper Carboniferous) was originally included in the family Cacurgidae. However, in *Cacurgus* Handlirsch, 1911, the type genus of this family, ScP is not distally fused with the multibranched RA, originating in the basal third of the wing. *Cacurgulopsis* and *Taiophlebia* seem to be sister genera and are therefore included in the family Taiophlebiidae (Dutra *et al.* in press).

Taiophlebia niloriclasodae Martins-Neto, sp. n.

Fig. 10

Etymology: Anagram derived from Nilson, Lorelai, Rita, Claus, Sonis, and Daiana, dynamic students of Geosciences Department, Universidade do Vale do Rio dos Sinos–UNISINOS, leadered by Dr Tania Lindner Dutra, the team that collected the holotype.

Description: Fore wing 104 mm long and 34 mm wide, as preserved, with straight costal margin and slightly acuminate apex. Subcostal area notably wide close the base, progressively narrowing toward the apex. ScA well-defined with numerous secondary veinlets and anastomosed pattern of cross-veins. ScP long with at least two strong secondary branches and several, relatively long, distally dichotomous veinlets, unbranched. RP origin at 1/5 of wing base. RP slightly sigmoid, with five secondary branches. MA long, slightly sigmoid, three-branched. MP+CuA origin little before RP origin level with at least eight terminal branches, clade-like. CuP two-branched with CuP1 being the smallest, converging to MP+CuA, fusing distally; CuP partially preserved, oblique to anal margin, reaching it at about 1/3 of wing base. AP1 fuses to AP2 close to the wing base, Y-shaped. AP1+2 parallel to CuP2. Intense pattern of cross-veins forming mosaics of heterogeneous cells in the whole preserved wing. No ornamentation pattern.

Holotype: BRAZIL: *Santa Catarina State*: Taió municipality; Upper Carboniferous, Itararé Subgroup, upper part of the Rio do Sul Formation. Housed at Geosciences Department, UNISINOS, Rio Grande do Sul, Brazil.

Taiophlebia ferreirai (Pinto, 1994), **comb. n.**

Archaemegaptilus ferreirai Pinto, 1994: 107–108, fig. 1 (holotype BA-PB-638, studied).

Remarks: *A. ferreirai* from the Upper Carboniferous (Piedra Shotle Formation, Chubut) of Argentina, was originally attributed to the palaeodictyopterans but clearly exhibits characters typical for *Taiophlebia*, and can be therefore transferred to the latter genus.

Superfamily Cacurgoidea Handlirsch, 1911

Several Carboniferous families were established on very fragmentary material and therefore their exact systematic positions and affinities are far from clear. The family Cacurgidae Handlirsch, 1911 was originally proposed for *Cacurgus* Handlirsch, 1911 from the Pennsylvanian of Mazon Creek, Illinois (USA). Carpenter (1943) as well as Brauckmann and Koch (1982) included *Heterologus* Carpenter, 1944 from Mazon Creek and *Heterologopsis* Brauckmann & Koch, 1982 from the Upper Namurian of Germany in this family. *Cacurgulopsis* Pinto & Adami-Rodrigues, 1995 from the Boituva locality (Paraná Basin, Upper Carboniferous of Brazil, discussed above) was additionally included by Pinto and Adami-Rodrigues (1995). However, *Cacurgus*, the type genus of the family, has ScP not distally fused with RA, a multibranched RA, origin of RP about 1/3 distally from the wing base, and therefore shows characters which are completely distinct from *Heterologus*, *Heterologopsis, Cacurgulopsis* and *Taiophlebia*, all of them with ScP and RA distally fused, unbranched RA, multibranched RP and origin of RP about 1/5 from wing base. Other families (Ampelipteridae Haupt, 1940 for *Ampeliptera* Pruvost, 1927, from the Upper Namurian of The Netherlands; Omaliidae Handlirsch, 1906 for *Omalia* van Beneden & Coemans, 1867 from the Westphalian of Belgium; and Carpenteropteridae Pinto & Ornellas, 1991 for *Carpenteroptera* Pinto, 1990) have the origin of RP 1/3 to 1/2 the distance from the wing base.

Family Carpenteropteridae Pinto & Ornellas, 1991

Cacurgonarkemidae: Pinto 1990: 7 (not based on valid genus name).
Carpenteropteridae: Pinto & Ornellas 1991: 93.

Diagnosis: See Pinto (1990: 7).

Carpenteroptera Pinto, 1990

Carpenteroptera: Pinto 1990: 7.

Type species: *Carpenteroptera onzii* Pinto, 1990, by original designation.

Diagnosis: See Pinto (1990: 7).

Species included: *C. onzii* Pinto, 1990 and *C. rochacamposi* (Pinto & Ornellas, 1978), comb. n.

Carpenteroptera rochacamposi (Pinto & Ornellas, 1978), **comb. n.**

Narkemina rochacamposi: Pinto & Ornellas 1978: 312, pl. II, figs 4a, b (holotype MP-I-5286; Rio Grande do Sul, Upper Carboniferous; in UFRGS; studied); Storozhenko 1998: 72.

Remarks: When describing *C. onzi*, Pinto (1990) pointed out the similarity of this species to the previously described *N. rochacamposi* Pinto and Ornellas, 1978. Judging from the published drawings, *N. rochacamposi* and *C. onzi* belong to the same genus, *Carpenteroptera*, and, after new knowledge (in particular on intraspecific variation) from the whole complex, maybe to the same species. But this decision cannot be made at this stage, because *C. rochacamposi* was based on a very fragmentary specimen, and it is impossible to compare it in detail with the more completely preserved *C. onzi*.

ACKNOWLEDGEMENTS

We cordially thank Prof. Dr Irajá Damiani Pinto (Porto Alegre-RS, Brazil) and Prof. Dr Karen Adami-Rodrigues (now Cruzeiro do Sul-ACRE, Brazil). OFG would like to express his thanks to Dr Sergio Archangelsky (Buenos Aires, Argentina) for providing us with important literature, as well as, Dr Silvia Césari and Dr Pedro Gutiérrez (MACN, Argentina) for their help and comments on the Bajo de Véliz palynology and age. Gustavo Barrios (UNNE, Argentina) is acknowledged for preparing the digital photos. In addition, CB would like to express his sincerest thanks to his South American friends and colleagues (in particular: Irajá Damiani Pinto and his team, Karen Adami-Rodrigues, Julián Petrulevicius, and the co-workers of the present article) for making him a fan of Gondwana matters. On the other hand, RGMN would like to express his sincerest thanks to his friends CB and OFG, the former for the friendship and expressive contribution to palearthropodology, including important remarks in this contribution and the special Clausthal team, and to the latter also for friendship and unconditional support; to Julián also for everything; to Irajá and Karen as special friends; to Denis Brothers for his efforts to see me in Pretoria. We are in essence a big family. OFG would like to express his thanks to Dr Silvia Césari (MACN, Argentina) for her help and comments on the Bajo de Véliz palynology and age. All authors are specially grateful for the opportune comments and suggestions made by Prof. Alexander Rasnitsyn (Russian Academy of Sciences, Moscow) and Dr Sergei Storozhenko (Far Eastern Branch of the Russian Academy of Sciences, Vladivostok).

REFERENCES

Archangelsky, S. & Cúneo, R. 1984. Zonación del Pérmico continental argentino sobre la base de sus plantas fósiles. *In*: *Memoria del III Congreso Latinoamericano de Paleontología*. México: APA, pp. 143–153.

Archangelsky, S., Arrondo, O.G. & Leguizamón, R.R. 1995. Floras Palaeozoicas. *In:* Stipanicic, P.N. & Hünicken, M.A., eds, *Revisión actualización de la obra paleobotánica de Kurtz en la República Argentina. Actas de la Academia Nacional de Ciencias en Córdoba* **11**: 85–125.

Archangelsky, S., Sabattini, N., Aceñolaza, F., Buatois, L., Gonzalez, C., Garcia, G., Césari, S., Ottone, E., Cúneo, R., Hünicken, M., Mazzoni, A. & Gutiérrez, P. 1996. Capítulo X. Paleontología bioestratigrafía de las Cuencas Paganzo, Calingasta-Uspallata San Rafael. *In*: Archangelsky, S., ed., *El Sistema Pérmico en la Argentina en la República Oriental del Uruguay*. Córdoba, Argentina: Academia Nacional de Ciencias, pp. 177–201.

Azcuy, C.L. & Jelín, R. 1980. Las palinozonas del límite Carbónico-Pérmico en la Cuenca de Paganzo. *In*: 2do Congreso Argentino de Paleontología y Bioestratigrafía y 1er. Congreso Latinoamericano de Paleontología, Buenos Aires 1978. Actas **4**: 52–68.

Azcuy, C.L., Andreis, R.R., Cuerda, A., Hünicken, M.A., Pensa, M., Valencio, D.A. & Vilas, J.F. 1987. Cuenca Paganzo. *In*: Archangelsky, S., ed., *El Sistema Carbonífero en la República Argentina*. Córdoba, Argentina: Academia Nacional de Ciencias, pp. 41–99.

Beneden, van, P.J. & Coemans, E. 1867. Un insecte et un gasteropode pulmoné du Terrain houiller. *Bulletins de l'Academie Royal des sciences, de lettres, et des beaux-arts de Belgique* (series 2) **23**: 384–401.

Béthoux, O. & Nel, A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Othoptera sensu nov. *Zootaxa* **96**: 1–88.

———2005. Some Palaeozoic 'Protorthoptera' are 'ancestral' Orthopteroids: major wing braces as clues to a new split among the 'Protorthoptera' (Insecta). *Journal of Systematic Palaeontology* **2** (4): 285–309.

Brauckmann, C., Brauckmann, B. & Gröning, E. 1996. The stratigraphical position of the oldest known Pterygota (Insecta, Carboniferous, Namurian). *Annales de la Société géologique de Belgique, Hommage à Maurice Streel* **117** (1): 47–56.

Brauckmann, C. & Koch, L. 1982. Neue Insekten aus den Vorhalle-Schichten (oberes Namurium B) von Hagen-Vorhalle. *Dortmunder Beiträge zur Landeskunde, Naturwissenschaftliche Mitteilungen* **16**: 15–26.

Carpenter, F.M. 1943. Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Illinois State Museum, Scientific Papers* **3**: 1–20.

Dutra, T.L., Chaves, R., Silva, S., Boardman, D., Fallgatter, C., Meucci, N., Lima, L. & Martins-Neto, R.G. In press. Taiophlebiidae n. fam. (Grylloblattida, Narkeminidea n. sensu), a new insect family for Itararé Formation (Paraná Basin, Upper Carboniferous), Taió locality (Santa Catarina State, Brazil): systematic and phylogenetical implications. *Gaea*.

Flores, M.A. 1969. El Bolsón de las Salinas en la provincia de San Luis. *Actas de las Cuartas Jornadas Geológicas Argentinas* **1**: 311–327.

Gorochov, A.V. 2001. On the higher classification of the Polyneoptera. *Acta Geologica Leopoldensia* **52/53**: 11–56.

Gutiérrez, P. 2006. Bajo de Véliz. *In*: Gutiérrez, P.R., Ottone, E.G. & Japas S.M., eds, *Léxico Estratigráfico de la Argentina. Volumen VII. Pérmico. Asociación Geológica Argentina, Serie B (Didáctica y Complementaria)* **28**: 202–203.

Gutiérrez, P. & Césari, S., 2000. Palinología de la Formación Bajo de Véliz (Pérmico Inferior), San Luís, Argentina: revisión sistemática y consideraciones bioestratigráficas. *Ameghiniana* **37** (4): 439–462.

Handlirsch, A. 1906–08. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Leipzig: Engelmann.

———1911. New Palaeozoic insects from the vicinity of Mazon Creek, Illinois. *American Journal of Science* **4** (31): 297–326.

Hünicken, M.A. & Pensa, M. 1975. Estratigrafía y tectónica de los depósitos gondwánicos del Bajo de Véliz (provincia de San Luis, República Argentina). *Revista de la Facultad de Ciencias Exactas, Físicas y Naturales, Sección C Geología* **3**: 1–37.

Hünicken, M.A., Azcuy, C.L. & Pensa, M. 1981. Sedimentitas paleozoicas. *In*: *Geología de la Provincia de San Luis.* VIII Congreso Geológico Argentino, Buenos Aires, Relatorio, pp. 55–77.

ICZN, 1985. *International Code of Zoological Nomenclature*. Third edition. London: The International Trust for Zoological Nomenclature.

———1999. *International Code of Zoological Nomenclature*. Fourth edition. London: The International Trust for Zoological Nomenclature.

Kukalová-Peck, J. 1991. Fossil History and the Evolution of Hexapod Structures. *In*: Naumann, I.D., Carne, P.B., Lawrence, J.F., Nielsen, E.S., Spradbery, J.P., Taylor, R.W., Whitten, M.J. & Littlejohn, M. J., eds, *The Insects of Australia*. Vol. 1. Melbourne: University Press, pp. 141–179.

Kurtz, F. 1895. Contribución a la Palaeophytologia Argentina II. Sobre la existencia del Gondwana inferior en la República Argentina (Plantas fósiles del Bajo de Véliz, província de San Luis). *Revista del Museo de La Plata* **4**: 125–139.

Martins-Neto, R.G., Dutra, T.L., Nowatzki, C.H., Silva, S.M. da, Chaves, R.C., Stranz, A., Fallkatter, C.,. Boardman, D.R., Lima, L. & Neto, N.M. 2004. Novo registro de insetos do Carbonífero Superior (Grylloblattida, Narkeminoidea) na região de Taió, SC, em níveis da Formação Rio do Sul. *Paleo 2004, Porto Alegre, RS, SBP. Resumo das Comunicações*, p. 45.

Martynov, A.V. 1930. On Palaeozoic insects of Kuznetsk Bassin. *News of the Geological Exploration Head Office* [*Izvestiya Glavnogo Geologo-razvedochnogo upravleniya]* **49** (10): 1221–1248. (in Russian)

Menéndez, C.A. 1971. Estudio palinológico del Pérmico del Bajo de Véliz, provincia de San Luis. *Revista del Museo Argentino de Ciencias Naturales* "*Bernardino Rivadavia*" *e Instituto Nacional de Investigaciones de las Ciencias Naturales, Paleontología* **2**: 1–30.

Pinto, I.D. 1990. A new Upper Carboniferous paraplecopteran insect from South Brazil. *Pesquisas* **17** (1–2): 7–10.

Pinto, I.D. & Adami-Rodrigues, K. 1995. A new Upper Carboniferous insect from Itararé Subgroup, Paraná Basin, Brazil. *Pesquisas* **22** (1–2): 53–57.

———1999. A revision of South American Palaeozoic insects. *In*: *Proceedings of the First International Palaeoentomological Conference, Moscow, 1998.* Bratislava: AMBA Projects, pp. 117–124.

Pinto, I.D. & Hünicken, M.A. 1980. *Gondwanarachne*: a new genus of the order Trigonotarbida (Arachnida) from Argentina. *Boletín de la Academia Nacional de Ciencias de Córdoba* **53** (3–4): 308–315.

PINTO, I.D. & ORNELLAS, L.P. 1978. Upper Carboniferous Insects from Argentina, I – Family Diaphanopteridae (Megasecopteroidea). *Pesquisas* **10**: 87–95.

———1980. Upper Carboniferous Insects from Argentina, II – Family Narkemocacurgidae (Paraplecoptera). *Boletín de la Academia Nacional de Ciencias de Córdoba* **53** (3–4): 287–291.

———1991. Substitute names for the extinct families Narkemocacurgidae Pinto & Ornellas, 1978 and Cacurgonarkemidae Pinto, 1990. *Pesquisas* **18** (1): 93.

———1994. A new species of palaeodyctiopteran insecta from Piedra Shotle Formation, Upper Carboniferous, Argentina. *Pesquisas* **21** (2): 107–111.

———1995. Paleobotanical and Paleozoological age divergences íon South América strata. *Pesquisas* **22** (1–2): 46–52.

PINTO, I.D., PIÑEIRO, G. & VERDE, M. 2000. First Permian insects from Uruguay. *Revista Pesquisas em Geociências* **27** (1): 89–96.

PINTO, I.D. & SEDOR, F.A. 2000. A new Upper Carboniferous blattoid from Mafra Formation, Itararé group, Paraná Basin, Brazil. *Pesquisas* **27** (2): 45–48.

PRUVOST, P. 1927. Sur une aile d'insecte fossile trouvée au sondage de Gulpen. *Jaarsverstag van voor het nederlandsche mijingebied Heerlen* **1926**: 76–77.

RASNITSYN, A.P. 2002. Subclass Scarabaeona Laicharting, 1781. The Winged Insects (= Pterygota Lang, 1888). *In*: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects*. Dordrecht *etc*.: Kluwer Academic Publishers, pp. 75–82.

STOROZHENKO, S.YU. 1996. New Upper Carboniferous grylloblattids (Insecta, Grylloblattida) from Siberia. *Far Eastern Entomologist* **26**: 18–20.

———1997*a*. Fossil history and phylogeny of orthopteroid insects. *In*: Gangwere, S.K., Muralirangan, M.C. & Muralirangan, M., eds, *The bionomics of grasshoppers, katydids and their kin*. Oxton & New York: CAB International, pp. 59–82.

———1997*b*. Classification of the order Grylloblattida (Insecta), with description of new taxa. *Far Eastern Entomologist* **42**: 1–20.

———1998. *Systematics, phylogeny and evolution of the grylloblattids (Insecta: Grylloblattida)*. Vladivostok: Dalnauka. (in Russian)

WHALLEY, P.E.S. 1979. New species of Protorthoptera and Protodonata (Insect) from the Upper Carboniferous of Britain with a comment on the origin of wings. *Bulletin of the British Museum of National History (Geology)* **32** (1): 85–90.